

VI. *On some neglected points in the structure of the pupæ of Heterocerous Lepidoptera, and their probable value in classification; with some associated observations on larval prolegs.* By Dr. THOMAS ALGERNON CHAPMAN, M.D., F.E.S.

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DESULTORY and unrecorded observations of many years on pupæ were recently thrown into order and invested with a meaning by a study of the earlier stages of the *Adelidæ*, and I have since taken more accurate notes of the structure of the pupæ of many species. Such accurate record, however, is a tedious and laborious process, and to go over the whole ground, or even a large fraction of it, will involve many years' work, and require the combined energies of a number of observers. I have therefore thought it better to bring the subject forward in its present imperfect state, in order to direct attention to it, rather than wait an indefinite time for the comparatively small additions I should myself be able to make; and, whilst apologising for the want of a larger mass of material, I may say that the indefinite and unnoted work of many years enables me to handle the material I have with more confidence than its own amount might appear to justify.

Descriptions of pupæ are often very minute in various particulars, but it is curious that they are usually silent on the points that I desire to draw attention to. One consequence of this is, that almost every fact that I here report has had to be observed by myself, with no assistance from any published description. The reference to the pupa of *Nascia ciliaris*, described by Mr. W. H. B. Fletcher, is, indeed, almost the only exception, though I am indebted to various correspondents for materials for observation. This is one excuse for calling attention to the subject as early as possible. It is very desirable that these omissions may in the future be supplied, and

that the description of an interesting pupa may not be found wanting, as at present it constantly is, in just the most important particulars.

The pupæ of the great mass of Lepidoptera Heterocera are of one or other of two forms characterised by very distinct and decided characters; the exceptions are, in a few instances, amongst the *Tineina*: with regard to these, I require to obtain more material and devote more study to them before venturing to say whether they are aberrant forms of either of the two principal divisions, whether they include perchance connecting forms, or whether they represent other and distinct divisions of equal importance (except in numbers) with the two principal divisions; but I think it probable that instances of each of these cases present themselves. One thing is certain, that they prove—already perhaps sufficiently evident—that the *Tineina*, instead of being a homogeneous group like the *Geometræ* or the *Tortricina*, contains groups of equal importance, for classificatory purposes, with them, and is in fact a mere heading for a number of very different groups of unclassified affinities, agreeing only in consisting of individuals of small size.

Before describing in detail these two forms of pupæ, I may make the way clearer by first directing attention to what I have called the “free segments,”—that is to say, the segments of the pupa that preserve freedom of movement. It would, perhaps, be more accurate to describe incisions where movement is preserved. Thus in a *Noctua* pupa we find movement exists between the fourth and fifth, between the fifth and sixth, and between the sixth and seventh, abdominal segments; but such description is more cumbrous, and therefore more inconvenient, than to say simply that the fifth and sixth abdominal segments are “free,”—that is, preserve freedom of movement with the segments adjacent to them on both sides, and one has not to revert to the more accurate but more circumlocutory expression, except when movement remains in one incision only (as in *Cœnonympha pamphilus*) when there is no “free segment,” and the incision at which movement remains has to be stated.

I have not dealt with the butterflies, which require to be treated separately from the moths in this matter, as

their variations in free segments and correlated matters do not come into line with the moths at all. My observations on them have, indeed, been too scanty to do more than show that this is so. I can only say that, in a few species at least, one finds in *Lycænidæ* no movement, in *Satyridæ* one incision with movement, in *Pieridæ* and *Erycinidæ* one free segment, in *Nymphalidæ* and *Papilionidæ* two free segments.

With the exception, then, of two or three small groups in the *Tineina* (so far as my observations extend), the *Heterocera* fall, in the matter of "free segments," into the two great classes I have mentioned,—*viz.*, 1st, those in which the free segments are the fifth and sixth abdominal, and only these, in both sexes; 2nd, those in which the seventh abdominal segment is free in the male, fixed in the female.

The first group is remarkably uniform in this, and in certain correlated characters throughout; whilst the second presents, along with some very fixed correlated characters, considerable variations in various directions, especially in the number of forward abdominal segments which are free.

These two forms of pupa present other and remarkable points of difference from each other; many of these other characters may be grouped together, as associated with definite differences of structure. The pupa with segments 5 and 6 only, free in both sexes, is that we are most familiar with, say amongst the *Noctuæ*. Such a pupa presents a hard, strong, chitinous exterior. When the larval skin is cast, the appendages, legs, wings, &c., fall into their places, and lie together so as to form a smooth exterior, which becomes hard and solid, whilst the surfaces that are hidden by being applied against each other have but a delicate pupal skin, represented, when the moth emerges, by a few flimsy shreds, whose previous position is almost impossible to determine, so that the empty pupa-case consists almost entirely of that portion which formed the outer covering. Such a pupa has been named "obtectæd," and was the pupa in view when the pupa of *Lepidoptera* was so described.

The pupa with the seventh abdominal segment free in the male, on the other hand, presents characters that bring it into line with those of bees and beetles. It is, to a great extent, "incomplete."

These two divisions agree so far with the division into Macros and Micros that one might almost be satisfied with those names for the pupæ and the groups they characterise, and I have learned to so regard them so far as to often use these names. There are, however, sufficient exceptions to make it desirable perhaps to have another name, and I will use those just suggested as being most descriptive. The first form of pupa (Macro) I will call "obtectæ," and the group which presents it "*Obtectæ*" (Macros); the other pupa "incomplete," more strictly semi-incomplete, and the group of moths presenting it "*Incompletæ*" (Micros).

The semi-incomplete pupa is of course familiar to every lepidopterist, but I believe little notice has been given to its peculiarities beyond noticing its motility and the dorsal spines that facilitate its movements, and especially it has been regarded, in each family where it occurs, as a special variation from some allied obtectæ form, whereas the truth appears to be that, wherever it occurs, it presents certain characters that show that its possessors belong to a separate division from the *Obtectæ*,—that it is probably a lower form, although many families of the *Incompletæ* have, in different directions, acquired higher characters than many of the *Obtectæ* have; such as the *Zygænidæ* in one direction, the *Pterophoridæ* in another, and the *Lithocolletidæ* in a third. Of these characters, none is more constant or more interesting—not only in itself, but in having, so far as I am able to point out, no necessary connection with the incomplete type—than the freedom of the seventh segment in the male; nor am I aware that attention to it has hitherto been directed.

In the pupa of the *Incompletæ* (Micros) the exposed surface is often perhaps less solid than in the *Obtectæ*, but at any rate the pupal skin of covered surfaces is much stronger than in them, and on emergence of the imago hangs together, so that the nature of each portion is rarely difficult to determine, and some portions, as in *Tortricæ* for instance, the inner wing-coverings, the portions of segments 2 and 3 (abdominal) covered by the wings and their intersegmental membranes, are only a little less firm than the coverings that are fully exposed. We here want a term to describe the process of breaking up of the pupa-case on the emergence of the moth, and

I find "dehiscence"—a term employed in Botany to describe the method in which the seed-vessels break up for the escape of the seed—meets the occasion.

On dehiscence these covered portions of the incomplete pupa become more or less fully exposed, and the appendages show an independence of each other quite at variance with ideas formed from the dehiscence of the obtected (Macro) pupa. In some *Tineæ*, even before emergence, the appendages and segments of the pupa—though apparently fused together—separate, on the least violence being applied, almost as perfectly as they would in the imago, without any fracture or tearing occurring: this would be quite impossible in an obtected (Macro) pupa.

The pupa of *O. antiqua*, female, interestingly illustrates the obtected pupa, and the fixity of the character of the fifth and sixth abdominal segments only being free; the wings and appendages are so short as not to reach the fourth abdominal segment, which might thus very easily be free, but there is no movement between it and the third either before or after dehiscence.

Certain other characters of the pupæ of the group with the seventh abdominal segment free in the male, which result from, or rather constitute, their "incomplete" structure, may now be noted.

In this pupa the head-coverings separate from the rest of the pupa in dehiscence, yet remain attached to one another in one piece,—that is, the plate covering the head and eyes; the antennæ-cases and the cases of the mouth parts separate from the rest of the pupa in one piece. In the Macro pupa these parts usually separate from each other; the head-cover is often one piece; the two antennæ-cases are separate, and the mouth-pieces may be separate, but more usually the mouth-pieces remain in one portion with the leg-coverings, and the antennæ-cases either with these or with the wings; whilst in the few cases (in Sphinges, Notodonts, and allied Bombyces) in which the head-coverings remain in one piece, they do so because they remain attached to the leg- or wing-coverings; they never remain in one piece when detached from the rest of the chrysalis-case. And similarly for the other segments in the *Incompletæ*, the pupal coverings of the wings, legs, &c., separate more or less from each other and retain their attachments

to their own proper segments, so that the empty pupa-case affords very often more information, as to the true relations of its several parts than the living pupa does.

Another aspect of this same peculiarity presents a feature in the dehiscence in which the Macro and Micro pupæ often markedly differ. An empty Macro pupa shows at once that the fifth and sixth abdominal segments were free, and no others; but an empty Micro pupa leaves much doubt as to which were free segments, because at many places, where no movement was allowed in the pupa, movement has taken place in dehiscence. Thus in *Tortrices*, where the free segments are four, five, and six (and seven in male), on dehiscence it would appear as if the wings were partially free from segments 2 and 3 (of abdomen), and as if these segments were free.

If an empty Micro pupa be examined,—and for this purpose *Cossus* and *Sesia* are most convenient, from their large size,—the cover of any appendage is found to be nearly perfect; the antennæ-case, for instance, is a tube with an opening on the inner surface close up to the head, through which the antenna has been withdrawn: in a Macro pupa it is a plate only, the inner side of the tube may or may not present just a discoverable shred of membrane.

Here an interesting observation presents itself by the way. The eyes of nearly all lepidopterous pupæ have an outer portion cut off by a sharp line from the upper and inner portion; and usually this outer portion is smooth and glassy, whilst the inner is rough, or at least similar to the rest of the pupa. Scudder ('*Butterflies of New England*,' p. 1554) has a short excursus on this subject, and regards this glazed eye as a remains of an ancestral pupal eye, and says it occupies the position of the line of larval ocelli. Now the dehiscence of the Micro pupa exhibits this piece as having no connection whatever with the head or eyes, but as belonging to the prothoracic segment. At any rate, what may be observed is this:—The antennæ-cases are removed from the groove in which they lie, the first portion of which is across the prothorax; the pupa-cover of the prothorax is continuous under this groove, and terminates in front in this glazed eye, which separates completely from the head (including true eyes), legs, &c., and forms a tip to

the prothoracic case. The prothorax is dorsally so degenerate a structure in *Lepidoptera* that the same divisions in it, as in the meso- and meta-thorax, cannot be made out in the imago, and in the obtected pupa it is covered by one plate, divided into two lateral portions. But in the *Incompletæ* (Micro) there is a very narrow plate, best seen after dehiscence, between this portion and the head, and it is with this plate that the glazed eyes are connected. If with this knowledge in hand one examines a Macro (obtected) pupa, not too near to the period of emergence, we find that from the surface line dividing the glazed from the true eye, a very strong dissepiment descends, showing here also that the two portions, though so closely and constantly associated, belong to quite different sections of the insect. I am not, of course, prepared to assert that this anterior portion of the prothorax may not have some less simple relationships, and may not be found to throw some light on the question, that is often suggested by the larva, whether the anterior portion of the second segment, which is dorsally a double one, does not ventrally contribute to supply portions of the head.*

The nature of the incomplete (Micro) pupa may be further illustrated by the way in which the long antennæ of *Adela* and *Gracilaria*, and some others, when they project beyond the other appendages, each remains separate and free to its extremity, and the same occurs as to the posterior legs in some cases; whilst in Macros (*Obtectæ*) long antennæ are carried carefully round the margin of the wing (*N. ciliaris*, *D. applanata*), or a long proboscis is doubled up in a projection (*Sphinx*, *Cucullia*), and so on.

Among the other characters that distinguish the Micro pupa is one which is closely associated with the semi-incomplete nature, that is, the mobility of the

* Mr. Poulton has most kindly shown me certain drawings, which, with some observations they suggest, appear to prove that the inner semilunar portion of the glazed eye is the true eye both of larva, pupa, and imago, and on such a point Mr. Poulton's authority is unquestionable. What I have regarded as part of the dorsal prothorax would therefore prove to be really part of the head. In any case, what I am just now most concerned to show, *viz.*, that there is a remarkable difference here, in structure and dehiscence, between the obtected and incomplete pupa, remains unaffected.—T. A. C.

Micro pupa. No Macro pupa leaves its cocoon or other place of pupation for the emergence of the moth; though this would often appear to be a desirable accomplishment, as, for instance, for the *Nonagrias*, the *Chilos*, the *Acronyctas*, that bore into wood or the many *Noctuæ* and others that bury themselves deeply in the soil for pupation. The Micro pupæ all do this, and are armed with various rows of hooks and spines on the abdominal segments to facilitate the process. To this rule the *Pterophori* form an exception. They have a free seventh male segment, and in dehiscence are true Micros, yet the pupa is fixed.

There is another distinction in habit between Macros and Micros that is possibly accidental, as it is by no means a universal one; still it is the case that Macros love to hibernate as pupæ. Micros very much avoid doing so. I say possibly accidental, because there are many families in both groups in which different species hibernate in different stages, and not a few genera even in which such a variety of habit is found; therefore, if this habit was originally a distinction between the two forms, it is not surprising that it has been broken in upon in many directions. But it seems probable that the semi-incomplete Micro pupa is inherently less adapted to hibernation than the fully obtected Macro. Many Micros pass the winter as larvæ in their cocoons, changing to pupæ in the spring. Among the Macros (*Obtectæ*), this habit is only common among the Pyrales. A curious illustration of this peculiarity is recorded by Mr. Healy in E. M. M., vol. iv., p. 10, in the case of *Antispila* (a true Micro, and probably indeed belonging to the *Adelidæ*). *Treitschkiella* passes the winter in its cocoon as a full-fed larva, but *Pfeifferella* as a pupa; but the moth begins to develop within it at once, and is well advanced before winter is fully set in, so that the hibernation is not truly that of a pupa. *Lithocolletes* (and *Gracilaria*?) present the largest proportion of instances of hibernating pupæ of any Micro genera; it is a curious coincidence that these have the first four abdominal segments fixed as in Macros.

In examining the mouth parts of the pupæ of certain *Adelids* (*Lampronia*, *Incurvaria*, *Adela*, &c.), I found a structure that was new to me, and which to avoid theory I called the "eye-collar." It is a narrow strip lying

transversely immediately below the eye, and stretching from the maxillæ to the antennæ, and comparable in width with the antennæ or tarsi. I suspected it to clothe some mouth part, but the curious thing was that it did not appear to unite with the mouth parts, though closely approaching them, but seemed to come from beneath the antenna. The possibility that it was some appendage of the prothorax was thus suggested. I then found the same organ in the pupa of *Sesiidæ* (*Bembeciformis*, *Tipuliformis*, and others), and, looking to the size of *Bembeciformis*, felt sure I should have no difficulty in determining what the "eye-collar" really was. In the meantime I had submitted the problem to our great authority on pupal morphology, Mr. E. B. Poulton, but he had not met with the structure, and was unable to suggest what it was. When *Bembeciformis* was ready to emerge, and also on emergence, I carefully examined this structure, and whilst disappointed in the hope of determining the question, found the problem much more interesting by the circumstance that this pupal structure did not contain any imaginal part, but was empty. I succeeded, however, shortly after, in solving the problem, by means of the pupa of *Nepticula*, in which the "eye-collar" is very well developed. It proved to be the case of the maxillary palpus, and the appearance of coming not from the mouth, but from under the antennæ and passing inwards, was in agreement with the actual fact. The palpus 5- (or 6-?) jointed, on leaving the maxilla, passes backwards in the angle between the head and prothorax, until it is situated deeply beneath the antenna, then it turns forwards to the antenna, and only reaches the surface by emerging from beneath the antenna and turning inwards, forming the "eye-collar," which contains only its terminal joints, the others being concealed deeply.

The greatest interest of this observation perhaps consists in the light it throws on the relationship of *Sesiidæ* and others, showing that they are descended from ancestors with well-developed maxillary palpi, which are still retained in the pupal state.

The "eye-collar" is also well developed in the *Cochliopodidæ*, which in many respects closely approach *Nepticulæ*, and in almost the whole Tineal section.

As to the maxillary palpi, indeed, I do not know any

facts that would actually contradict an addition to the definition of *Obtectæ* and *Incompletæ* that would state the former to be without maxillary palpi, the latter to have them, or some trace of them at least, in the pupa state.

The very simple maxillary palpi of Pyrales would appear to be an exception to this. They are less apparent in the pupa than in the imago. Traces at least of jointed maxillary palpi always exist in a Micro pupa.

The development of the maxillary palpi will deserve a special research. *Lithocolletes* is the only form of *Incompletæ*, except *Pterophorus*, and in some degree *Zygæna*, in which the "eye-collar" is difficult to detect in the pupa, whilst many families possess a largely-developed "eye-collar," whose imagines have no maxillary palpi. In these there exists, therefore, theoretically, a 5- or 6-jointed maxillary palpi. In *Obtectæ* no maxillary palpi are seen in the pupa, and in those Pyraloids that possess one it is small and simple, and does not reach the surface in the pupa.

I have suggested that these characters probably have much value for purposes of classification. This idea arises from the circumstance that they are apparently very constant throughout each family, and thus suggest a classification that happens to be nearly identical with that now accepted; that they confirm certain more or less recent movements of groups or families to fresh positions; and that where they are at variance with accepted classification, it is usually with reference to small groups whose present position is already held to be open to much doubt.

The true Macros are at once separable from the remaining *Obtectæ* by a larval character, but I have not succeeded in determining a corresponding character in the pupa. In the Macros proper the full-grown larva has the hooks of the abdominal (4 ventral pairs) prolegs developed only along their inner margin, whilst in the remainder (Pyraloids?) the hooks form a complete circle on the four pairs in 7, 8, and 9, and 10 segments (3, 4, 5, and 6 abdominal). I am not aware that any absolute diagnosis of Macro-Heterocera has hitherto been given, though every tyro believes in its existence.

The structure of the prolegs has received too little attention, and I do not know that anyone has noted that it differs in different families. A. S. Packard, in a recent

paper, appears to refer to all that has been written on the subject, and it does not amount to much.

My own observations are still very imperfect, and the subject, like that of the pupæ, is a large one, with room for a great deal of work. The best records of individual species I am acquainted with is that in Scudder's 'Butterflies of New England,' a work which is a model in many other respects.

I think one finds in the *Adelidæ* some indications of how the prolegs and their hooks were developed. If, as is perhaps hardly probable, they do not present us with the actual history of their development, they, by reversion or some other process, give us what are probably some of the stages. In *Eriocephala* (*Micropteryx pars*) there are no prolegs. In *Nemotois* (*fasciellus*) and *Adela* (*rufimitrella*) there are series of chitinous points, beautifully arranged in rows like the teeth of a shark, the larger in front, those in each row alternating with those in the next rows, and gradually getting smaller till they merge in the fifth or sixth row in the ordinary integumental points. In the ordinary position of each proleg there are two such sets of points facing each other along a transverse line (only the anterior set in segment 10). In *Incurvaria muscalella* the prolegs have two rows of hooks, facing each other in this way along a transverse line. In *Lampronia capitella* the young larva has no hooks, but the full-grown larva has hooks placed in a circle, yet with gaps showing that they are still an anterior and posterior set.

In *Tortrices* the row of hooks is usually double; that is, there are longer and shorter hooks, but they are always in one perfect row; but in other families we find that traces of the multiple rows of *Nemotois* persists. This is the case in *Hepialus*. In *Sesiidæ* again the circle of hooks is flattened antero-posteriorly, and weak or wanting at the outer and inner ends, showing a relationship to *Incurvaria*.

The anal prolegs very rarely have more than the anterior half developed. In *Hepialus* the circle is fairly complete.

The *Crambidæ* have hooks of alternate size like *Tortrix* (as have other *Pyaloids*), *Crambus* often (always?) has 3 sizes of hooks alternated in one row.

Though it is outside my brief, I cannot help referring

to the case of the *Hesperidæ*, that in their three rows of hooks show a persistence of Adelid (or at least very low) structure, whilst the true butterflies (adult larvæ) have the same structure as the true Macros.*

The proleg then seems to reach its full development with a complete circle of hooklets. A higher development of the insect is accompanied by a fuller development of the inner half of this circle, but by the degeneration and disappearance of the outer half. This may often be followed out in Macros, where the young larva has Pyraloid prolegs, which often suddenly (at one moult), or more gradually (in two or three) assume in the full-grown larva the unilateral Macro (proper) type.

I think there can be little doubt, since it accords with conclusions arrived at on other grounds, that the highest Lepidoptera-Heterocera are those that possess unilateral prolegs in their first stages. This is the case in (some at any rate) *Sphinges*, *Notodonts*, &c., and also in *Nycteolidæ*, recently promoted, but for long kept among the *Tortrices*. They are, however, true Macros, and of a high type, probably as high as the *Sphinges*, but probably in no way related to them. The pupæ are wholly unlike any Micros, and are of strictly Macro type, with fifth and sixth abdominal segments free.

The true Macros thus defined (pupa with only fifth and sixth abdominal segments free, adult larva with only inner half of proleg furnished with hooks), correspond precisely with those usually so called, including *Nycteolidæ*, *Nolidæ*, *Deltoides*, &c., with the exception of a group of Micros that have been placed with them only on account of their size, and whose relationship to each other has been at length recognised by getting them all close together, though they are nearly related to each other in no other way than that they are all Micros (*Incompleteæ*). These are the *Zygenidæ*, *Sesiidæ*, *Cossidæ*, *Zeuzeridæ*, *Cochliopodidæ*, and the *Psychidæ*, if the latter are not already by common consent placed with the *Tineæ*.

The other sections of *Obtectæ*—the Pyraloids—include the Pyralids, Phycids, Crambi, Eudoridæ, and certain

* Some pupæ of *Hesperidæ* I have seen look as if the 7th was, or had recently been, free in the ♂; but I have seen very few altogether.

groups usually placed in the *Tineæ*, some of which (like the *Gelechidæ*) are sufficiently allied to the rest of the group to be undoubtedly Pyraloids: others of which may be entitled to form groups of the *Obtectæ* of equal value with the Macros (proper) and Pyraloids. But here I must say that I have not examined enough species of each group, or minutely enough, to give more than a very provisional opinion. These groups are the *Epigraphiidæ*, *Hyponomeutidæ*, *Plutellidæ*, *Æcophoridæ*, *Argyresthidæ*, *Coleophoridæ*, and possibly a few genera of doubtful position.

I have not formed any strong opinion as to the value of the remarkable character of many Gelechid pupæ, by which the movement of the free segments is confined to an antero-posterior one only, with something of the manner that belongs to the movement of the click-beetles. There are several oddities among the Pyrales, and this seems hardly a sufficient one to require a distinct class.

Of the Pyraloid families mentioned above, the *Hyponomeutidæ*, *Argyresthidæ*, and *Coleophoridæ*, seem to be those that are most probably of value corresponding to the Macros (proper) and Pyraloids, whilst the others rather fall in line with the other families of Pyraloids. As to this I am by no means confident, but the *Coleophoridæ*, for instance, have a pupa of by no means the hard texture of a Macro or Pyraloid, and it is not cylindrical, having on each side of the dorsum a deep hollow so that a cross section presents re-entering angles.

Finally, there is *Alucita*.

It is curious that in all these groups, whether they be classed as Pyraloids in one group or separately, the larvæ have 16 legs, and complete circles of hooks on abdominal prolegs, differing in this way from the Macros (proper) where we have groups with 14 and 12 and 10 legs (missing legs lost), and from the Micros (*Incompletæ*), where variations occur even to an apodal state (missing prolegs often (?) never acquired). I think it is also true that though nearly all are more or less concealed feeders, leaf-miners are wanting, or very rare.

The Micro (*Incompletæ*) pupæ are more interesting than the Macros, in so far that they present much more variety. Their incomplete character suggests that they are a lower form than the *Obtectæ*, and this is confirmed

by their close resemblance to many tipulid pupæ, especially those of some gall-gnats, a resemblance that appears to be one of relationship rather than accidental, from the dipterous pupa having hind wings, although the imago has halteres, and from the imago presenting scales of quite a lepidopterous character.

In the *Micros* the number of free segments varies, the 7th is always fixed in the female and free in the male, except in *Hepialus*, when the 7th segment tends to become fixed in the male, and I am not sure that it is always quite free in all *Gracilarias*, but in both these cases the pupa is in other respects so typically *Micro* and related to other species in which the 7th (male) segment is free that no doubt of their position can arise.

Another character, that of free mobility, is also universal, except in the *Pterophorids*, which are typical *Micros* in "incompleteness," dehiscence, and 7th male segment.

This character of the *Pterophori* probably entitles them to the highest place in the division. There is, however, a competitor on another ground, *viz.*, the *Zygænidæ*. In the *Obtectæ* (*Macros*) we found the higher portion, the *Macros* proper, distinguished from the *Pyraloids* and others by the character of the abdominal prolegs, *viz.*, that they had hooks only on the inner sides. This same distinction obtains in the *Zygænidæ*, which are thus parallel with the *Macros* (proper).

This character of prolegs is no doubt correlated with the habit of feeding externally. The complete circle, with feeding internally or under a web, between united leaves, &c. The external habit is very rare amongst the *Micros*, and indeed only exists, besides the *Zygænidæ*, in the *Cochliopodidæ*, where it has been met in a different manner: and in *Micropteryx* (*calthella*), which possesses well-developed true legs (and anomalous abdominal legs). These three families are therefore close together. The free segments of *Zygæna* and *Limacodes* are the same (3456—34,567), and the curious appendages in *calthella* larva may represent the urticating organs of *Cochliopod* larvæ. Among the *Macros* proper the internal and concealed feeders retain the true *Macro* structure, and must be supposed to be descended from external feeders, and to have reverted to the ancient

habit, without having regained the correlated structure so far as the prolegs are concerned.

Zygæna has the 3rd and 4th, 5th and 6th (and 7th in ♂) abdominal segments free; it very markedly opens the other incisions on dehiscence, and has the other characters of a Micro dehiscence—head parts united together and separate from the others, internal pupal coverings very distinct, pupa emerges from cocoon, &c. It possesses ill-developed eye-collars (maxillary palpi). It is the only one I have noticed to retain the glazed eye with the head parts; they separate from the anterior prothoracic case, which is distinctly developed. The dehiscence is otherwise typically “incomplete.”

In *Pterophorus* the dehiscence is also characteristically incomplete, the free segments are (abdominal) 4, 5, and 6 in the female, 4, 5, 6, 7 in the male.

The remaining *Incompletæ* (Micros) are not very easily divisible, but appear to form two groups that we may call *Tortrices* and *Tineæ*, or rather *Tortricoids* and *Tineoids*, but I find a difficulty in stating any definite characters (pupal) to divide them. The best appears to be in the development of the maxillary palpi. In the *Tineæ* these are always well developed in the pupæ. In the *Tortrices* they are ill-developed or almost wanting. In *Cossus*, after dehiscence, the cases of the maxillary palpi are small but quite evident, and the same obtains in most *Tortrices*.

There are, however, a few *Tineæ* in which it is also ill-developed.

Perchance the *Tortricoids* and *Tineoids* should be taken as one group and divided according to the segments that are free, or a division might be made by defining the *Tortricoids* as having a row of spines along the hind margins of the segments. This would somewhat vary the grouping.

The *Tortrices* proper form the greater part of the section of *Tortricoids*. They are distinguished by having the 4th, 5th, and 6th segments free in both sexes, and the 7th also in the male, by having two rows of hooks for progression across the dorsum of each segment, and by the marked way in which the 2nd and 3rd (abdominal) segments become free on dehiscence, whilst retaining a modified attachment to the wing cases. There are still many genera of *Tortrices* that I have not

been able to examine, but there is so great a uniformity amongst those that I have examined that I hardly expect to meet among the others with any wide departure from the type. *Fabriciana* differs from *Tortrices* in the hinder set of dorsal points being wanting, in the 2nd segment not so markedly becoming free on deliscence, and in the wing cases projecting over 4th segment (though free from it), though this feature does occur in true *Tortrices*. The pedicellate legs of the larva also point to this family, though very close to *Tortrix*, being entitled to a separate place. The egg is very curious.

In *Cossus* I can find no character at any stage to distinguish it from *Tortrices*. The pupa may be taken as (very conveniently from its large size) showing the *Tortrix* character. The larva, with its circles of hooks of alternate lengths on the prolegs, is of strictly *Tortrix* pattern. The imago agrees with *Tortrix* in every detail, the venation is almost identical with that of *C. pomonana*, the palpi, spurs on legs, &c., are the same, the wing pattern closely resembles that of *Retinia*, to which its habits suggest it is probably closely allied. The dorsal structure of the metathorax in *Cossus* agrees absolutely with *Tortrix*, the metascutum being divided into two lateral parts that just meet in the middle line without uniting. In nearly all true Macros these two portions are widely separate, whilst they unite in the middle line, forming one piece in certain *Tineæ* only, especially *Adelids*. It is of interest to find that this same Tineal conformation is strongly marked in *Hepialus*, and less so in *Sesia* and *Limacodes*. I am indebted to Dr. Wood for calling my attention to this interesting point; it is one we have yet done little more than glance at, though it is referred to by several authorities.

Zeuzera and *Hepialus* differ from *Tortrix* in having the 3rd abdominal segment free, but in a peculiar and modified manner: the wing cases project over it, and appear to be fixed to it, but really the incision between it and 2nd is bent backwards as it passes towards the ventral surface, a very unusual modification of structure, which impedes the free movement of 3 on 2. In *arundinis* the dorsal spines become less developed posteriorly. Of *Hepialus* I have not been able to get abundant material, but certain pupæ, apparently males, have the 7th segment fixed, or nearly so; if this is so, it is clearly

related to the very unusual immense ventral flange on that segment and the great dwarfing of segments 8, 9, and 10. These and all the other characters of *Hepialus* would lead one to place it very distinctly from *Cossus*, yet there appear to exist in Australia many forms uniting *Cossus*, *Zeuzera*, and *Hepialus* into one family, both in their imaginal and pupal characters, and it must be in Australia that the derivation of a Hepialid form from an Adelid one, and of *Tortrix* from the *Cossus* side of the group, must be worked out. No doubt intermediate forms do or did exist between any two families that may be named, and therefore that we know many of them in any particular case, as that of *Cossus* and *Hepialus*, should not prevent us regarding these as tolerably wide apart.

The metathoracic structure of *Hepialus* came as a very unexpected confirmation of the idea that of the Tortricoid group it was the nearest to the lower Adelids, and, despite its specialisation, was near the line by which *Tortrix* was derived from some Adelid form.

Since the removal of *Cossus*, &c., from the *Bombyces* to the *Micros* will have to meet a great deal of what has become almost instinctive belief, I may mention one or two further points supporting the *Micro* character of these families. To take, first, the pupa: there is in the pupal outline of the *Micros* (*Incompletæ*), viewed laterally, a strong tendency to form a waist by the sinking in dorsally of the 5th segment (1st abdominal); this is almost unknown in the *Macros* (*Obtectæ*). This is well seen in *Cossus* (as in all *Tortrices*). *Bembeciformis* presents this character markedly.

The wing-patterns of all (? *Arctia*, &c.) true *Macros* consist of transverse lines in certain well-known positions, and of certain stigmata. These do not exist very distinctly in many of the *Pyraloids*, except, perhaps, true *Phycids*, and are wholly wanting in all *Incompletæ*. The *Adelidæ* may be taken as showing the fundamental pattern in these, a uniform colour strongly tending to be metallic, and with markings in irregular patches and spots (*L. rubiella*); the more definite pattern of *L. capitella* also obtains largely amongst *Micros*. Now, none of these families—*Zygæna*, *Cossus*, *Sesia*, &c.—present the *Macro* pattern; *Zygæna*, the highest of them, has even retained the metallic tints of *Adela*, and is marked by

irregular blotches. These also occur in *Zeuzera*, and are extraordinarily developed, as well as metallic surface, in some exotic *Hepiali*. The blotching in *Zeuzera* seems to have settled down into transverse striation in *Cossus*, from which the passage through *Retinia* to *Carpocapsa* is easy to some of the definite (but far from Macro) patterns of *Tortrix* markings.

When we come to the Tineoid section of the Micros, or true *Tineina*, I must assert that my ignorance greatly exceeds my knowledge; that is to say, that I have examined several species of all the larger genera, and have examined a good number of other genera, but there are still genera of which I know nothing; and whilst I do not expect these will alter the general outline, they will no doubt throw considerable light on some details, and will probably present some interesting and anomalous forms, as it is amongst these that the largest variety exists, both in the larval and pupal states. Here almost every genus presents a slightly different type, whilst among the Macros (true) an extensive field affords only one type; and among the *Tortrices* it seems to be much the same.

The Tineoid section of *Incompletæ* therefore wants study of larger material than I yet have, in order to say anything very decided about them.

In *Nepticula* we have as typical an example as any; the parts of the pupa separate readily on slight violence, so much so that it is not easy to be sure whether the first free segment is the 2nd abdominal or the 3rd, but I believe it is the latter. This is also the case in *Limacodes*, in *Tischeria*, and in Adelids. In *Tinea* and in *Sesia*, and in *Psychidæ*, the first free segment is the 4th, but I have not examined enough *Tineæ* to say that this is the rule in the genus. *Lithocolletes* and *Gracilaria* present the first four abdominal segments fixed as in *Obtectæ*, but in all other characters—7th free in male, dehiscence, mobility, eye-collar, &c.—they are typical *Incompletæ*. *Gracilaria* shows free extremities to legs and antennæ in some instances. In *G. elongella* there seems to be a tendency to the 7th segment becoming fixed in the male; when I say a tendency, I have seen some male pupæ (empty) in which I could not satisfy myself that it was free, though distinctly so in others.

As there are many genera of the *Tineina* of which I

know nothing, the following list will probably be lengthened; but I may note certain species as not, so far as I have yet studied them, clearly belonging to either of the sections (*Obtectæ* and *Incompletæ*); *Elachistidæ* (*Tischeria* belongs to *Incompletæ*); *Perittia*, *Lyonetidæ* (*Bucculatrix* belongs to *Incompletæ*; the free segments are 4, 5, 6 (and 7), eye-collar not detected). To go into any detail as to these till the structure of many more species has been noted would be of little use.

I think it is probable that the association of the Sesiids with the Tineids will not meet with much objection. I have already referred to the well-developed maxillary palpus of the pupa as a remarkable confirmation of this position, as well as to the Tineid character of the larval prolegs. But possibly a little more detail as to *Limacodes* may be required. In many respects *Limacodes* and *Nepticula* seem extremely different; apart from the matter of size, the former is an external feeder. Then the venation of *Nepticula* is crippled by the minute size of the moths, so as to render them very different, though probably not essentially so in this respect. It is therefore somewhat surprising to find a resemblance that is almost identity in the pupa. In both the pupal skin is very delicate; the free abdominal segments begin at the 3rd, if not at the 2nd; the appendages are easily separated, as they might be in a bee or beetle pupa; the dorsal spines are arranged in several rows of small equal points towards the dorsal margin of the segment. The maxillary palpus (eye-collar) is strongly developed, large and obvious in *Testudo*; in *Asellus* it stretches right across from the antennæ to the mouth-parts, and on dehiscence remains attached to the head coverings. It is, indeed, larger proportionally in these species, where it is obsolete in the imago, than in *Nepticula* or others, where it persists in the imago. The pupa emerges from the cocoon in much the same manner, and leaves a very delicate pupa-case, in which, after the manner of the *Incompletæ*, the covered parts are nearly as strong as the exposed.

The larva passes the winter in a passive state in the cocoon, changing in spring; whilst its apod character might be explained by its very recent descent from a footless mining larva. The urticating properties of sundry exotic species of the group may perhaps be

allied in nature to the secretion by some of these miners, and especially *Nepticula*, of some poison that retards the autumnal decay of the leaf they inhabit.

The imago is without maxillary palpi, but the pupa proves this to have been quite recently lost. When we examine the metathorax, the anterior section (scutum) has at first sight a Macro structure, that is, there are two well-developed lateral portions; but on close observation these are found to be continuous in a narrow but distinct chitinous ridge, such as does not occur in any of the Macro section of the *Obtectæ*.

Nepticula and *Limacodes* present us, indeed, with the *Incomplete* pupa in an extreme form; the empty pupa-skin has every segment and each appendage quite free from the others. The dorsal armature consists, in Cochliopods, of a number of rows of very fine spines, all belonging to one series. In the species of *Nepticula* I have examined there are no spines to the hind margin, but the anterior set is in some species a single row of largish spines, in others two rows and three rows; in the latter instances the spines are much smaller. There is therefore a variability in the armature that might easily extend to include the Cochliopod form.

Nepticula, however, has one character that I have not met with elsewhere, *viz.*, the antennæ-cases on dehiscence divide into the cover of the first joint and that of the remainder, each separate from the head, yet still held together sufficiently to keep their places fairly.

I have only had a portion of a pupa-case of *Micropteryx* (*calthella*), so do not like to insist further than I have already done on the association (from larval characters) of *Zygæna*, *Limacodes*, and *Micropteryx*.

In *Sesia* the larval prolegs, the strong development of the maxillary palpi, and the continuity in the imago of the anterior section of the metathorax across the middle line, appear to determine its place among the Tineoids in spite of some Tortricoid characters, such as the posterior dorsal rows of spines.

Though I have, regarding this communication as largely preliminary, omitted detail wherever I could, as, for instance, I see I treat *Alucita* in four words, though this covers the rearing of a number from the egg and the examination of some dozens of pupæ, I ought, perhaps, to note the ova of *Zygæna* and *Lima-*

codes. The former has a very delicate transparent shell, and the whole egg looks so soft and unprotected that it seems more suited for the internal situation of an Adelid egg than the exposed position in which it is laid; whilst that of *Limacodes asellus* is a flat, colourless, transparent speck, much like that of *Nepticula*, but not resembling that of any true *Bombyx*.

I have specially avoided notice of those *Tineinæ* that appear to present some indications of transition between the *Obtectæ* and *Incompletæ*. But of those that are in no sense transitional, it is interesting to note, in the *Pyrales*, the possession of maxillary palpi, and the habit of hibernating as full-fed larvæ, characters much commoner in *Incompletæ*; and in the *Lithocolletes*, on the other hand, the obsolescence of the maxillary palpi, the habit of hibernating as a pupa, and the loss of freedom in the first four abdominal segments. Remaining, however, true *Incompletæ* in the free 7th male segment, in mobility, in dehiscence, and in the facility with which the appendages separate in a sound pupa.

I have endeavoured to show the leading points in a tabular form, but, like all linear arrangements, it does not give the proper values to the several facts, emphasising some and slurring over others.

I hope some day to go into details as to some of the families, when I have material to more fully work them out; but I hope that others more able will in many instances forestall me.

To summarise the facts here brought forward. There are two very distinct types of pupæ in the *Lepidoptera-Heterocera*, each presenting such a constant set of characters that the members of each group must be more closely related together than to any of the other group.

This shows the true relationships of the group of *Macros* (?) *Zygæna*, *Sesia*, *Hepialus*, *Cossus*, &c.

It also shows the *Pterophorids* to be unrelated either to *Pyraloids* or to *Alucitids*.

It shows some of the directions in which the *Tineina* must be divided.

The existence of a well-developed maxillary palpus in sundry pupæ whose imagines are without it.

A certain amount of light on the relations of the glazed eye.

A definite diagnosis of *Macro-Heterocera*.

LEPIDOPTERA-HETEROCERA.

- A.—OBTECTÆ.**—Pupa smooth and rounded, externally solid, inner dissepiments flimsy. Free segments in both sexes 5th and 6th (abl.). Never emerges from cocoon, or progresses in any way. Dehiscence by irregular fracture.
- 1.—**Macros.**—Larva with hooks of ventral prolegs on inner side only. (Exposed feeders.) *Sphinges, Bombyces, Nolida, Nycteolida, Noctuina, Geometra.*
 - 2.—**Pyraloids.**—Larva with complete circle of hooks to ventral prolegs. (Concealed feeders.) *Pyrales, Phycida, Eudorida, Crambida, Gelechida, Plutellida, Ecophorida. (Epigrahiida, Alucitida.)*
 - 3.—————?.—Doubtful whether Pyraloids or of separate (classificatory) value. *Hyponymenida, Argyresthida, Coleophorida. (Perittia?), (Elachistida?).*
- B.—INCOMPLETÆ.**—Pupa less solid and rounded, appendages often partially free. Free segments may extend upwards to 3rd (abdominal). 7th always free in male, fixed in female. Dehiscence accompanied by freeing of segments and appendages previously fixed. (Except in 1) pupa progresses and emerges from cocoon.
- 1.—Pupa attached by cremaster. Free segments. 4 5 6 7. 4 5 6. *Pterophorina.*
 - 2.—Pupa free to move and emerge from cocoon.
 - a.—Larva concealed feeder, often miner, and usually rather active when not cramped by mine.
 - 1.—Free segments. 5 6. 5 6 7. *Lithocolletida, Gracilariida.*
 - 2.—Free segments. 4 5 6. 4 5 6 7.
 - a.—TINEÆ (*Tincida, Psychida, Sesiida*).
 - b.—TORTRICES (*Tortricina, Cossus, Exapate, Simæthis*). (*Castnia*.)
 - 3.—Free segments. 3 4 5 6. 3 4 5 6 7.
 - a.—ZEUZERA and HEPIALUS tend to lose 3rd as a free segment (are gaining it as a fixed segment?).
 - b.—TISCHERIA.
 - c.—ADELIDÆ. Ovipositor (of imago) formed for piercing plant-tissues.
 - d.—NEPTICULIDÆ. Antennæ separate from head in dehiscence.

b.—Larva exposed feeder. Slug-like in form and movements, head very retractile. Free segments. 3 4 5 6 7.
3 4 5 6.

1.—MICROPTERYGIDÆ.* Eight pairs abdominal legs, curious appendages, moss feeders.

2.—COCHLIOPODIDÆ. Legs evanescent, but traces of extra pairs and of curious appendages. Max. palps large in pupa, not in imago.

3.—ZYGÆNIDÆ. Legs of Macro type. Max. palps evanescent in pupa.

C.———?.—Pupa with no free segments, appendages adherent to all abdominal segments. *Lyoutia*, *Cemiostoma*, *Bedellia*.

NOTE.—*Eriocephala* (*Micropteryx purpurella*, &c.) appears by imaginal characters to belong to *Adelidæ*. But the pupa is truly *Incomplete*, not semi-incomplete, as all the other *Incompletæ* are,—that is, the appendages are all absolutely distinct and free, and all the abdominal segments are “free”; moreover, it possesses working jaws.

* I have only seen a portion of a pupa of these, and of Psychids I have had none of my own, and have not been able to examine them freely.—T. A. C.